AGE-RELATED TIMING OF MIGRATION: GEOGRAPHIC AND INTERSPECIFIC PATTERNS

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ABSTRACT.—Differential timing of passage by age or sex classes at sites along migration routes is ambiguous with respect to whether these groups differ in onset or rate of migration and provides little insight into the dynamics of differential timing. Therefore, we compared age-specific differences in timing of autumn migration by five species of passerines at three sites in eastern North America. Two species showed consistent differential timing of migration at all sites, with adults preceding immatures in Red-eyed Vireos (*Vireo olivaceus*) and immatures preceding adults in Magnolia Warblers (*Dendroica magnolia*). Age differences in timing of passage by Swainson's Thrushes (*Catharus ustulatus*), American Redstarts (*Setophaga ruticilla*), and Common Yellowthroats (*Geothlypis trichas*) varied with year and location. The degree of differential timing varied substantially among sites within species. For Swainson's Thrush and Magnolia Warbler, species which breed largely to the north of all three sites, there was little evidence for differential rate of migration between age classes. Only the Red-eyed Vireo and Magnolia Warbler showed evidence of differential onset of migration. Our results point to the need for further data on the dynamics of differential timing as a prerequisite for testing hypotheses on the causes of differential migration. *Received 1 Dec. 1995, accepted 1 Sept. 1996.*

Differential migration among individuals of the same species may involve differences in migratory timing (review by Gauthreaux 1982), distance migrated (reviews by Gauthreaux 1982, Ketterson and Nolan 1983), or both (e.g., Chandler and Mulvihill 1990a, Nolan and Ketterson 1990). Because ornithologists have a long tradition of quantifying the timing of passage by migrants at sites along migration routes, patterns of differential timing are particularly well-known. Differential timing may occur between sexes (e.g., Annan 1962, Johnson 1965, Bildstein et al. 1984, Francis and Cooke 1986, Chandler and Mulvihill 1990a), between recognizable age classes (e.g., Johnson 1965; Hussell et al. 1967; Hussell 1980, 1991; Bildstein et al. 1984; Chandler and Mulvihill 1990a), or among populations of different geographic origin (e.g., Mueller et al. 1981, Högstedt and Persson 1982, Hedenström and Petersson 1984).

Most studies of differential timing in passerines have documented differences in the timing of passage at a specific site. Unfortunately, timing of passage at a single site along the migration route is ambiguous with respect to whether groups (ages, sexes, or populations) differ in onset of migration, rate of migration, and/or site of origin (Chandler and Mulvihill 1990b). Nevertheless, data on the processes that underlie patterns of dif-

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ferential timing are needed to identify the causes of differential timing—causes that have received remarkably little attention despite the recent revitalization of interest in avian migration.

The purpose of this paper is to explore patterns of age-specific differential timing of migration in several species of passerine birds and to discuss the processes that may account for these patterns. Specifically, we quantified geographic (three sites in eastern North America), interspecific (five species), and temporal (two years) patterns of age-specific differential timing of fall migration. Our objectives were (1) to compare migratory timing of adult and immature passerines among several species of passerine birds, (2) to determine whether these patterns are consistent across space and time, and (3) to assess whether these data can be used to provide information on the onset and rate of migration in species that exhibit differential timing of migration. We show that comparisons of migratory timing over a broad geographic area may provide insights into the mechanics of migratory timing and discuss the importance of this information to an understanding of the causes of differential migration.

STUDY AREAS AND METHODS

Study sites.—We assembled data on the timing of autumn migration from three sites in eastern North America. The most northern site was Long Point Bird Observatory (LPBO; 42°33'N, 80°10'W) on the north shore of Lake Erie, Ontario, Canada. The second site was Powdermill Nature Reserve, field station of the Carnegie Museum of Natural History, in western Pennsylvania (PNR; 40°10'N, 79°16'W). The third and southernmost site was Bon Secour National Wildlife Refuge, located on the western tip of Fort Morgan peninsula in coastal Alabama (FTMN; 30°10'N, 88°00'W). These locations were selected for two reasons. First, these sites (separated by 12° of latitude) lie along a migration route for birds moving out of northeastern North America to the Gulf of Mexico where they may take either a circum- or trans-gulf route into the Neotropics. The timing of passage by birds at these sites should be broadly representative of a variety of Neotropical migrants. Second, daily banding operations at each site provide detailed records of migratory timing. A description of banding operations at LPBO can be found in Hussell (1991) and at PNR in Leberman and Wood (1983). At FTMN, approximately 25 12-m mist nets were opened daily throughout the autumn migration in forest and scrub habitat (Woodrey 1995).

Data collection.—We selected five species for analysis: Swainson's Thrush (*Catharus ustulatus*), Red-eyed Vireo (*Vireo olivaceus*), Magnolia Warbler (*Dendroica magnolia*), American Redstart (*Setophaga ruticilla*), and Common Yellowthroat (*Geothlypis trichas*). We chose these five species because identifiable age classes were captured in relatively large numbers at all three banding sites.

Birds included in the analysis (first captures only) were captured at each site during daily banding operations in autumn 1990 and 1991. Capture dates for the five species were 1 Aug.–17 Oct. at LPBO, 1 Aug.–19 Oct. at PNR, and 31 Aug.–31 Oct. at FTMN. Birds of these five species banded over these dates were considered migrants; we assume that any captures of local breeders were insufficient to affect our conclusions concerning differential timing of migration.

For those species whose breeding ranges lie largely to the north of all three capture sites

(Swainson's Thrush and Magnolia Warbler), we estimated average migration rates for adults and immatures based on the median capture dates of each age class at the three sites. This was done by dividing the distance between two sites by the number of days difference in median passage dates at the two sites (Ellegren 1990). These estimates are meant to be qualitative, since they are based on the assumption that the populations of these species sampled at LPBO and/or PNR were at least partially the same as those at FTMN. In short, we assume a simple NE-SW oriented migration route from LPBO and PNR to FTMN and into Central and South America. Although alternative migratory patterns are conceivable, our approach is to make an explicit simplifying assumption and generate testable generalizations about migration rates in the age classes of these two species. This method (comparison of median capture dates from sites along the migration route) has produced estimates of migration speed that compare favorably with rates calculated from direct banding recoveries (Ellegren 1990). The distance from LPBO to FTMN was calculated to be 1610 km; PNR to FTMN is 1380 km.

Statistics.—We used Mann-Whitney tests to compare differences in the capture dates (Julian dates) of adults and immatures at each of the three sites. The Mann-Whitney test is sensitive to differences in the location of the distributions of capture dates between age classes (Sokal and Rohlf 1995). All tests were two-tailed, and we used SYSTAT for all analyses (Wilkinson 1989).

We used box plots for the visual display of migratory timing. These plots convey substantial information about the shape of a distribution by displaying the median with a vertical line, the interquartile range (IQR; a box around the median), and adjacent values (extent of a horizontal line). The upper adjacent value is the observation less than or equal to the upper quartile value plus $1.5 \times$ IQR. The lower adjacent value is the observation greater than or equal to the lower quartile value minus $1.5 \times$ IQR. Observations that lie 1.5 IQRs or 3.0 IQRs beyond the quartile values are outside values and are shown with asterisks and open circles, respectively.

Because we conducted multiple tests (five species at three sites), we sequentially Bonferroni-adjusted (Hochberg 1988) p-values to maintain an experimentwise error rate of 0.10 within years (Chandler 1995). In 1990, all p-values that were significant when unadjusted, remained so after Bonferroni adjustment. In 1991, only two unadjusted values became nonsignificant after adjustment for multiple tests. Therefore, we report unadjusted values and indicate cases where adjustment for multiple tests would alter significance.

RESULTS

Swainson's Thrush.—In 1990, Swainson's Thrushes showed no significant difference in the timing of passage of adults and immatures at LPBO ($U = 8145$, $P = 0.46$), PNR ($U = 685$, $P = 0.09$), or FTMN ($U = 619$, $P = 0.14$) (Fig. 1). The same was true for 1991, with the exception of LPBO, where median passage of adults was significantly earlier than immatures ($U = 13,755$, $P = 0.002$; Fig. 1).

The general lack of significant age differences in passage of Swainson's Thrushes among sites suggests that migration rates of adults and immatures were similar (or do not differ sufficiently to result in differential passage over the range of latitudes analyzed here). Nevertheless, the age difference in median dates of passage varied from immatures preceding adults by 4.5 days at FTMN in 1990 to no difference at LPBO in 1990
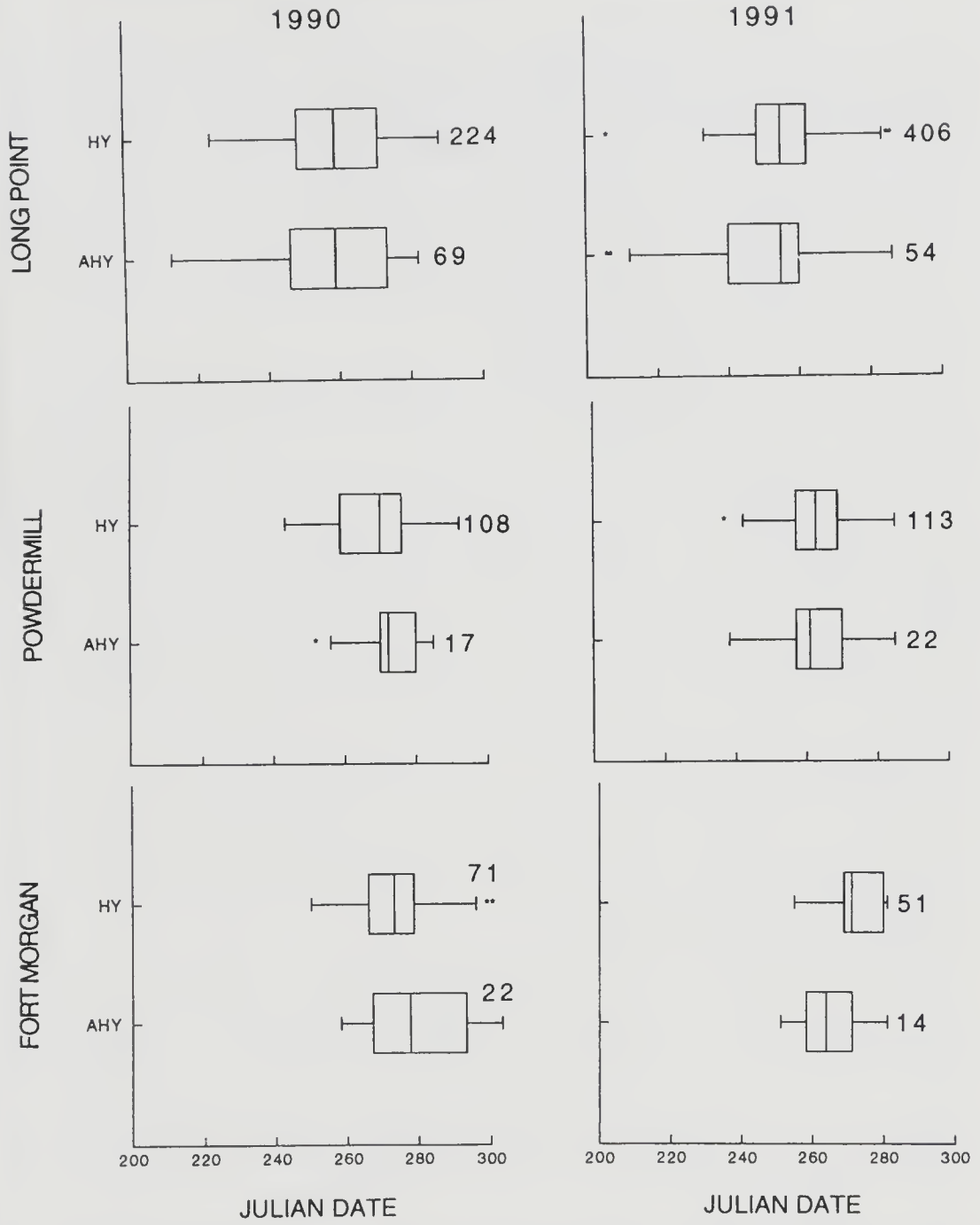
FIG. 1. Distribution of capture dates (first captures only) for Swainson's Thrushes at the three sites. Box plots display median (vertical line within box), interquartile range (extent of box), adjacent values (extent of horizontal line), and outside values (asterisks and open circles). Julian dates range from 18 July (200) to 26 October (300). Sample sizes are given to the right of each plot.

to adults preceding immatures by 7.5 days at FTMN in 1991 (Fig. 1). Passage dates at LPBO (averaged across years) suggested an average migration rate to the Gulf coast of 119 km/day for adults and 108 km/day for immatures. At PNR (again averaged across years), the estimates of migration rates were 402 km/day for adults and 317 km/day for immatures. The large difference in estimated migration rates from LPBO and PNR was attributable to a large difference in passage dates of Swainson's Thrushes at these two sites (7–13 days later at PNR even though these sites are separated by only 235 km).

Red-eyed Vireo.—Adult vireos migrated significantly earlier than immatures at all three sites in 1990. Median passage dates of the age classes differed by 21 days at LPBO ($U = 917$, $P < 0.001$), 22 days at PNR ($U = 8766$, $P < 0.001$), and 17 days at FTMN ($U = 1065$, $P = 0.004$) (Fig. 2). The age differences in timing of migration were so large in 1990 that the median passage of adults at FTMN preceded median passage of immatures at LPBO. The pattern was similar in 1991 but less pronounced. Adults preceded immatures by four days at LPBO ($U = 1456$, $P = 0.04$), 13.5 days at PNR ($U = 2256$, $P = 0.001$), and two days at FTMN ($U = 1205$, $P = 0.06$) (Fig. 2). After adjustment for multiple tests, only the PNR difference was significant.

Estimates of migration rates were complicated by the extensive breeding range of this species. Like Swainson's Thrushes, however, there was local variation in passage dates. Even though LPBO is just to the north of PNR, Red-eyed Vireos passed PNR 8–9 days earlier in 1990 and 11-20 days earlier in 1991 (Fig. 2).

Magnolia Warbler.—In 1990, adult and immature Magnolia Warblers differed significantly in timing of passage at all three sites. Immatures preceded adults by an average of 16 days at LPBO ($U = 2204$, $P < 0.001$), 10 days at PNR ($U = 1263$, $P < 0.001$), and 19 days at FTMN ($U = 359$, $P < 0.001$) (Fig. 3). The same was true in 1991, with immatures preceding adults by five days at LPBO ($U = 5259$, $P < 0.001$), 12 days at PNR ($U = 1292$, $P < 0.001$), and eight days at FTMN ($U = 186$, $P < 0.001$) (Fig. 3).

The median passage dates at LPBO and FTMN (averaged across years) suggested average migration rates of 79 km/day for adult Magnolia Warblers and 92 km/day for immatures. Median passage dates at PNR and FTMN gave estimates of 101 km/day for adults and 103 km/day for immatures.

American Redstarts.—In 1990, there were no significant differences in the timing of passage of adults and immatures at LPBO ($U = 1261$, $P = 0.07$), PNR ($U = 1115$, $P = 0.40$), or FTMN ($U = 1287$, $P = 0.91$) (Fig. 4). The
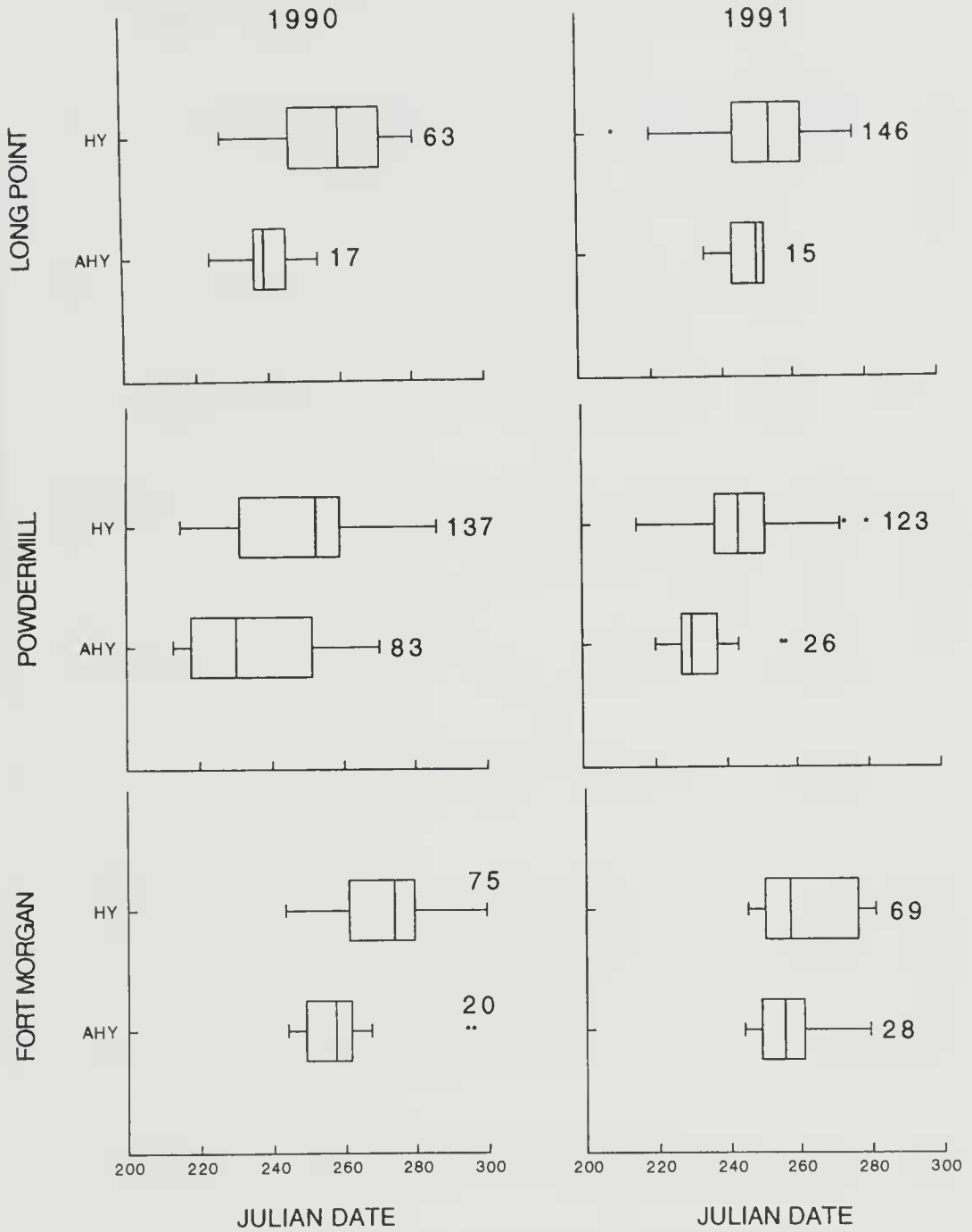
FIG. 2. Distribution of capture dates (first captures only) for Red-eyed Vireos at the three sites. See Figure 1 for description of box plots.

same was true in 1991, with the exception of FTMN where immature redstarts preceded adults by 10 days ($U = 2284$, $P < 0.001$) (Fig. 4).

Although the extensive breeding range of this species complicated inferences about migration rates, there was substantial among-site variation in passage dates. In 1990, the median passage date of adults was 13 days
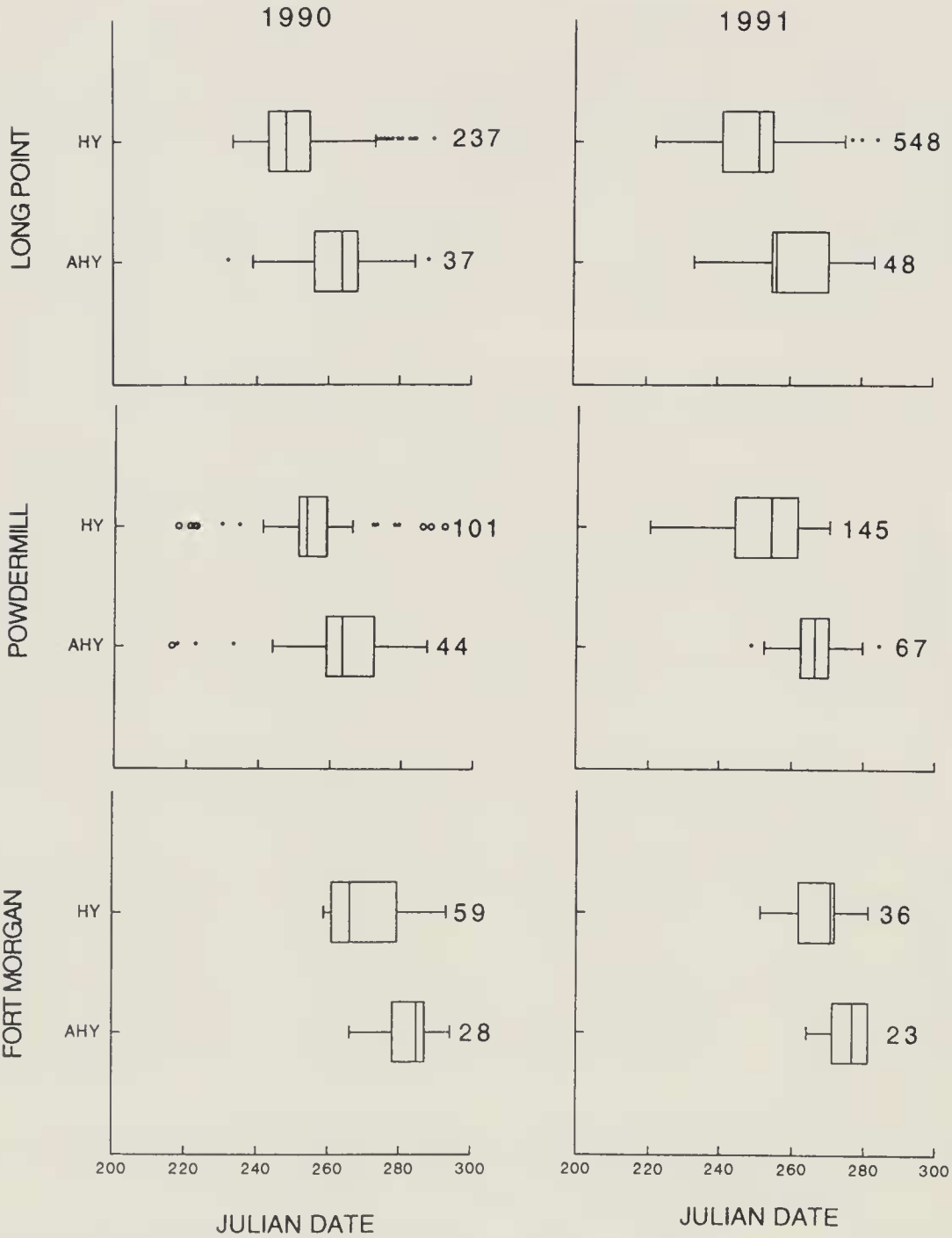
FIG. 3.   Distribution of capture dates (first captures only) for Magnolia Warblers at the three sites. See Figure 1 for description of box plots.

earlier at LPBO than at PNR just to the south; the median passage of immatures was only six days earlier at LPBO that same year. In 1991, the median date of passage for the age classes differed by no more than 3.5 days between these two sites (Fig. 4).

Common Yellowthroat.—Adult and immature yellowthroats did not dif-
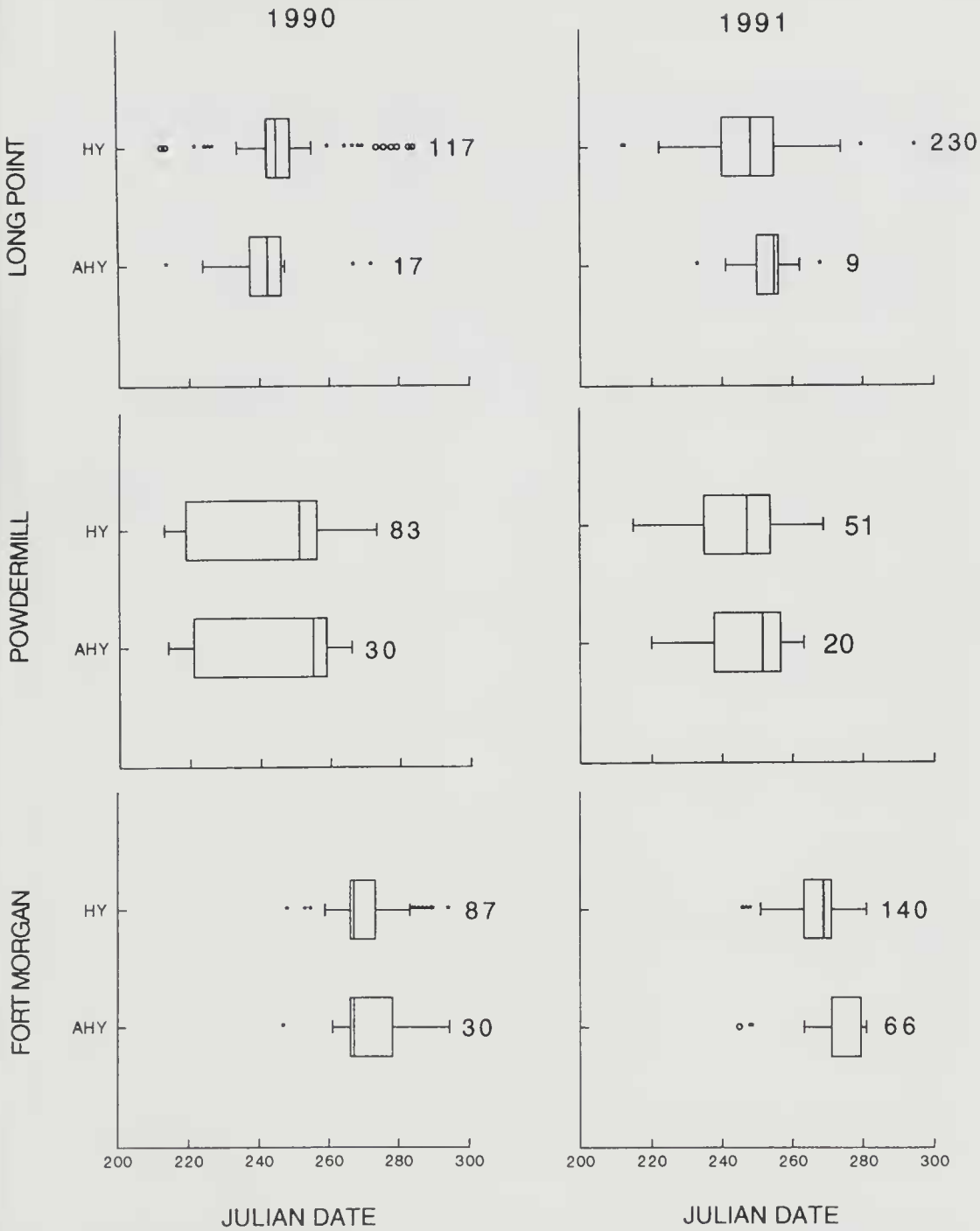
FIG. 4.   Distribution of capture dates (first captures only) for American Redstarts at the three sites. See Figure 1 for description of box plots.

fer significantly in timing of passage at any site in 1990 (LPBO: U = 1637, P = 0.14; PNR: U = 7421, P = 0.53; FTMN: U = 1714, P = 0.95) (Fig. 5).

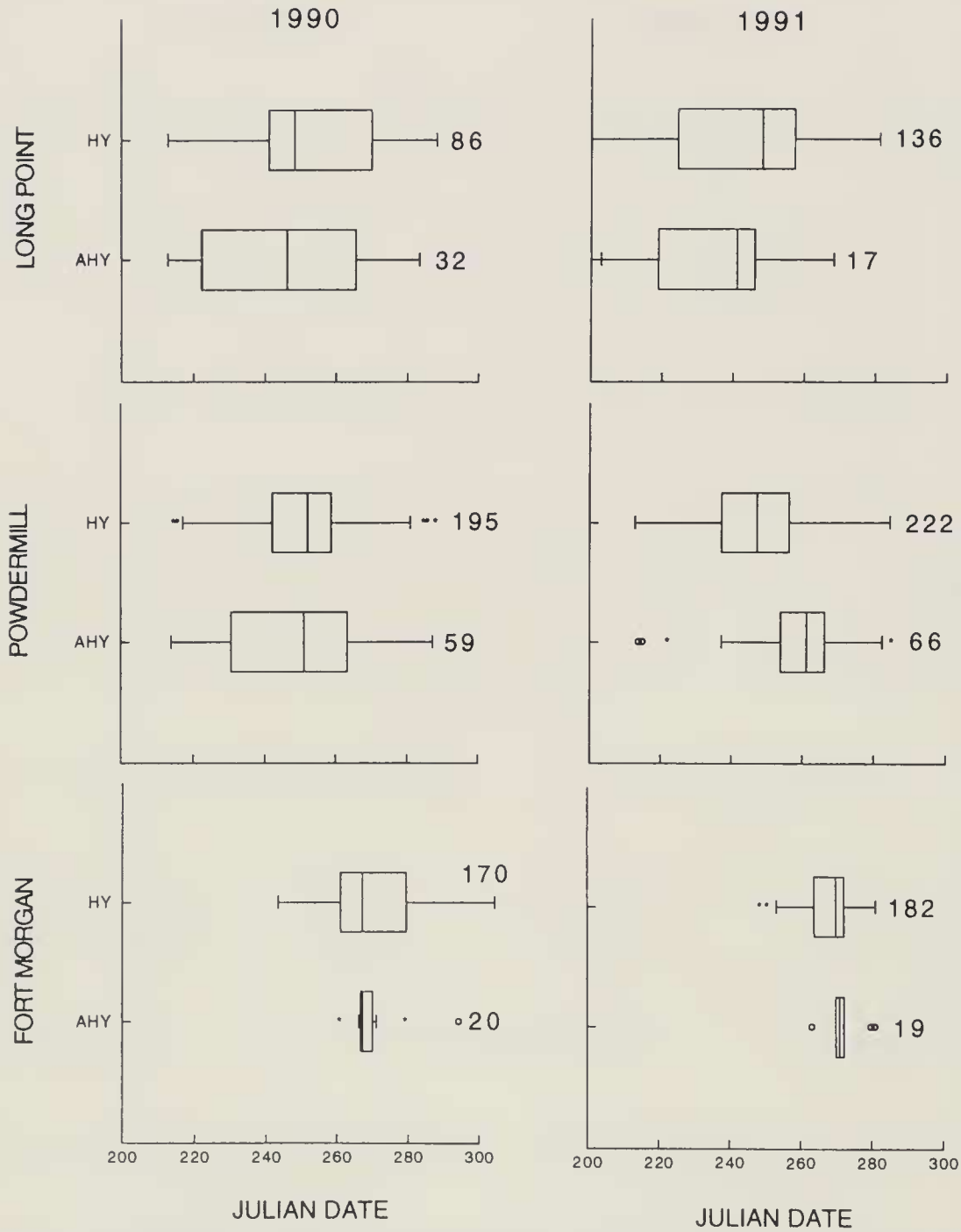In 1991, median passage of immatures preceded that of adults by 14

Fig. 5. Distribution of capture dates (first captures only) for Common Yellowthroats at the three sites. See Figure 1 for description of box plots.

days at PNR ($U = 3909$, $P < 0.001$), but there was no significant differential timing at the other sites (LPBO: $U = 1472$, $P = 0.07$; FTMN: $U = 1298$, $P = 0.07$) (Fig. 5). In 1991, adult yellowthroats passed LPBO 20 days earlier than at PNR just to the south (immatures had almost identical median passage dates at these sites; Fig. 5).

DISCUSSION

When analyzed on a large geographic scale, five species of passerine migrants showed different patterns of age-specific differential timing of migration. Adult Red-eyed Vireos preceded immatures at all sites, whereas the opposite was true for Magnolia Warblers. Age-specific differences in timing of passage by Swainson's Thrushes, American Redstarts, and Common Yellowthroats varied with site and year. Our results demonstrate that the magnitude of age-specific differential timing can vary substantially between years (e.g., Red-eyed Vireos) and that migratory timing can vary appreciably from site to site within a region (PNR vs LPBO). For those two species for which it was possible to estimate average migration rates, the rates were similar between adults and immatures (Magnolia Warbler) to perhaps faster in adults (Swainson's Thrushes based on PNR data).

The specific patterns of differential timing that we report from each site are not new (e.g., Leberman and Clench 1969, 1970). In fact, many studies document adults preceding immatures during fall migration (e.g., Hussell et al. 1967; Seel 1977; Hussell 1980, 1991; Chandler and Mulvihill 1990a) or immatures preceding adults (e.g., Mueller and Berger 1968, Nilsson 1970, Bildstein et al. 1984). However, simply documenting patterns of differential passage at a site along the migration route offers little insight into the dynamics of differential migratory timing within species of passerine birds (Chandler and Mulvihill 1990b). Comparative analyses of data from several sites along the migration route, such as that attempted here, offer the opportunity to explore the contributions of rate and onset to differential timing in passerines (Rosenfeld and Fagerström 1980, Hildén and Saurola 1982, Ellegren 1990).

Onset versus rate of migration.—Our data provide evidence for differential onset of migration in two of the five species that we examined. Magnolia Warblers showed large age differences in migratory timing at all sites. Because the bulk of their breeding range lies just to the north of LPBO and PNR, differences in rate of migration by age classes of Magnolia Warblers appear insufficient to account for the large differences in their timing of passage at LPBO and PNR. Apparently, immature Magnolia Warblers initiate migration approximately 1–2 weeks earlier than adults, depending on the year. Red-eyed Vireos also show large age differences in timing at all three sites although the magnitude of the difference varied annually. It is difficult to explain this age difference in timing of passage at all sites as a result of age-specific differences in rate of migration. Instead, adult vireos appear to depart the breeding grounds substantially earlier than immatures (possibly as much as three weeks).

This early departure may be related to the fact that adult Red-eyed Vireos show a very limited prebasic molt during late summer (Mulvihill 1993) that might permit earlier onset of migration. A substantial late-summer movement of second-year birds and/or failed breeders (R.S. Mulvihill, pers. comm.) also may be a contributing factor. Whatever the cause, age differences in timing of migration by Red-eyed Vireos appear susceptible to substantial annual variation (Fig. 2).

We also have some evidence on rates of travel by age classes in two of the five species. Assuming that one or both of our northern sites sample the same populations as our Gulf site (or at least populations with the same migratory timing), our results suggest that adult and immature Magnolia Warblers migrate at roughly similar rates (approximately 80–100 km/day). Swainson's Thrushes appear to migrate more rapidly than the warblers, and adults may migrate at a slightly faster rate than immatures (by about 80 km/day based on PNR data). If these age differences are real, they are insufficient to result in significant differential passage by the time Swainson's Thrushes reach the Gulf coast. We emphasize that these estimated rates are based on two seasons of data and are meant to be qualitative, testable generalizations about migratory dynamics within species. Ellegren (1990), in a similar study of Bluethroats (*Luscinia svecica*), found that immatures had slower migration rates than adults early in autumn migration (100 km/day vs 40 km/day) but not as they neared the wintering grounds (immatures approached 100 km/day). Unfortunately, Ellegren's study is rare in reporting age-specific estimates of migration rates in passerines. Our estimated migration rates of 80–130 km/day are generally similar to those reported for other passerines (Hyytiä and Vikberg 1973, Hildén and Saurola 1982, Ellegren 1990). This suggests that our comparisons of timing among sites produced reasonable estimates of migration rates for Swainson's Thrushes and Magnolia Warblers.

The only exceptions to this were our estimates of migration rates by adult and immature Swainson's Thrushes from PNR to the Gulf (402 km/day and 317 km/day, respectively). These large estimates are attributable to Swainson's Thrushes passing PNR almost two weeks later than LPBO just to the north (235 km). The passage dates at LPBO give migration rates for Swainson's Thrushes most similar to those reported in other passerines (Hildén and Saurola 1982), but little is known about movements between these two sites and the Gulf coast. These banding sites may sample different populations of thrushes, or individuals passing PNR could make rapid and direct flights to the Gulf while an ecological barrier at LPBO (Lake Erie) may slow movements or direct birds farther west. That there are interesting migratory dynamics at these sites is further suggested by Red-eyed Vireos moving through PNR 8–9 days earlier than

at LPBO (opposite of the pattern in Swainson's Thrushes) and the fact that age classes of American Redstarts and Common Yellowthroats vary substantially in their timing between the two sites.

Causes of differential timing.—A variety of causes might ultimately result in age differences in onset or rate of autumn migration (Table 1). First, differential timing might result from differential constraints operating on age classes. In other words, there is a single optimal migration schedule for all individuals of a population, but constraints operate differentially on adults and immatures. Second, there may be different optimal migration schedules for the age classes even in the absence of any differential constraints on these groups.

Constraints that might influence migration include age-related differences in timing of molt, which could impose different migration schedules (Rimmer 1988, Chandler and Mulvihill 1990a, Ellegren 1990). Molt that is completed on the breeding grounds should primarily influence onset of migration, whereas molt that extends into migration (or occurs en route; Rohwer and Manning 1990, Thompson 1991) could affect rate of migration. Age differences in molt would have to be pronounced to account for the large differences in onset of migration in Red-eyed Vireos or Magnolia Warblers. Nevertheless, adult Red-eyed Vireos have such a limited prebasic molt during fall (Mulvihill 1993) that it might not preclude a very early onset of migration (Cannell et al. 1983), and molt can delay the departure of adults from the breeding grounds by several days in some species of warblers (Yellow Warbler [*Dendroica petechia*]; Rimmer 1988). Molt also appears to hamper fat accumulation by Swainson's Thrushes at stopover sites (Winker et al. 1992). Overall, the possible costs of molt to fat accumulation rates or flight dynamics need to be quantified further before the influence of molt on differential migration can be tested adequately.

Lack of experience may also place important constraints on migratory timing in immature birds. Inefficient foraging, unfamiliarity with stopover sites, or less efficient navigation could all slow onset or rate of migration. However, lack of experience as a general explanation for slower migration in immatures is not well supported (but see Ellegren 1990). Lack of experience does not appear to preclude early departure from the breeding grounds by immature Magnolia Warblers and subsequent rates of migration comparable to adults. Furthermore, in redstarts and yellowthroats, immatures appear to have migratory timing equal to that of adults. Although inexperience is a fundamental feature of birds undertaking their first migration, specific tests of its effects on migratory timing are needed.

Social interactions might also affect migratory timing (e.g., Gauthreaux 1978, Nolan and Ketterson 1990). As was the case for experience, social

dominance needs further testing as a general explanation for age-specific differential timing. Virtually any observed pattern of age differences in timing could be consistent with the constraints imposed by social dominance. Young birds might leave the breeding grounds early to avoid dominant adults or late because reduced access to food in the presence of dominant adults slows fat accumulation. Along migration routes, immatures might move through stopover sites faster or slower for the same reasons. This is not to suggest that social effects on migratory timing are not important. Rather, these effects need to be tested in specific cases and not simply invoked as being consistent with observed patterns. We know of no data on the possible contribution of social interactions to the differential timing reported here.

Onset of migration in adult birds also might be slowed by the energetic demands of late summer breeding activity. This seems most likely in species raising multiple broods into late summer (immatures from early broods could initiate migration while adults are still occupied with breeding activity). Only the Magnolia Warbler showed differential onset of migration consistent with this constraint and this trait is not apparent in this species. We caution that early migration by failed breeders (as is possible in Red-eyed Vireos) might obscure any clear relationship between adult breeding activity and delayed migration. Finally, the well-documented differences in flight morphology between age classes (e.g., Alatalo et al. 1984, Mulvihill and Chandler 1990) might affect flight speeds, flight ranges, or fattening strategies and thus result in differential rates of migration.

In the absence of differential constraints between ages, there might still be differential timing of migration. Even with equal migratory options open to them, selection might still favor age classes departing the breeding grounds, arriving at stopover sites, or arriving on the wintering grounds at different times (Table 1). Although sexual selection for early arrival on the breeding grounds by males is a clear example of such differential selection, the selection pressures for different optimal migration times between ages during the autumn are less obvious. Migration schedules that are tied to late summer exploration in immatures (Ellegren 1990), to age-specific variation in latitudinal distribution (e.g., Ketterson and Nolan 1983), or to habitat segregation on the wintering grounds (e.g., Lynch et al. 1985) are possible sources of differential selection pressure on rates and onset of migration.

Overall, our results show that broad geographic comparisons of migratory timing can provide insight into the dynamics of differential migration. Quantifying onset and rate of migration permits more detailed analyses of migration strategies and narrows the possible causes of differential

TABLE 1

POTENTIAL ULTIMATE CAUSES FOR DIFFERENTIAL ONSET AND RATE OF MIGRATION BETWEEN
AGE CLASSES DURING AUTUMN MIGRATION

Onset of migration	Rate of migration
Differential constraints on timing imposed by:	
Molt on breeding grounds	Molt in transit
Experience	Experience
Social interactions	Social interactions
Breeding activity	Morphology
Differential selection for:	
Early arrival (destination, stopover)	Early arrival (destination, stopover)
Early departure (site of origin)	Early departure (stopover)

timing (Table 1). However, testing of specific causes of differential timing between age classes is hampered by a lack of information on age-specific timing of molts, effects of experience on migratory performance, and the role of social dominance in migratory movements. We hope this study and those such as Ellegren (1990) will stimulate increased attention to the dynamics and causes underlying differential timing of migration.

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